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# TEMPERATURE, WATER, AND RESPIRATORY REGIMES OF AN AMPHIBIOUS SNAIL, *POMACEA URCEUS* (MÜLLER), FROM THE VENEZUELAN SAVANNAH

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It has long been known (Troschel, 1845; Pelseneer, 1895; Prashad, 1925, 1932) that ampullariid or "pilid" snails possess "amphibious" respiratory structures, one part of the mantle cavity containing a ctenidium (the characteristic molluscan gill) and another part being modified as a gas-filled lung cavity. This double adaptation for aquatic and aerial respiration in *Pomacea urceus* is probably most important during the rainy season (Burky and Burky, in preparation). Respiration is amphibious in both its structural (Andrews, 1965) and its behavioral (Burky and Burky, in preparation) aspects. In addition, the annual sequence of rainy and dry seasons of the Venezuelan plains dictates an amphibious way of life for *Pomacea urceus* (Burky, in preparation).

Terrestrial snails face particular problems of temperature regulation and water balance since their moist bodies are exposed during activity (Howes and Wells, 1934a, 1934b; Hogben and Kirk, 1944; Dainton, 1954a, 1954b; Russell Hunter, 1964; Machin, 1964, 1965, 1966; Cloudsley-Thompson, 1968, 1970; Vernberg and Vernberg, 1970). The relationship of body temperature to environmental temperature has been reported for intertidal (Lewis, 1963; Fraenkel, 1968; Grainger, 1968; Davies, 1970; Newell, Pye, and Ahsanullah, 1971; Vermeij, 1971; and others) and for other terrestrial gastropods (Hogben and Kirk, 1944; Dainton, 1954a; and others). In deserts and in tropical areas with periodic dry seasons there are additional problems of high temperatures and limited water. Under arid conditions the body temperatures of the pulmonates *Helicella virgata* (Pomeroy, 1968) and *Trochoidea seetzeni* (Yom-Tov, 1971a) are a function of their position in the temperature gradient between air and ground as they aestivate attached to vegetation above the ground. When the pulmonate *Sphincterochila boissieri* is dormant on the ground surface, body temperature is primarily a function of slow conduction from the substrate and the transfer of body heat to the air (Yom-Tov, 1971a; Schmidt-Nielsen, Taylor, Shkolnik, 1971). For these pulmonates, the rate of water loss is too low to be of value for evaporative cooling. In desert snails the high reflectivity of light-colored shells is important in reducing the absorption of solar radiation (Yom-Tov, 1971a; Schmidt-Nielsen *et al.*, 1971). Some snails wait out severe climatic periods in the ground (Pain, 1950; Meenakshi, 1964; Coles, 1968; Pomeroy, 1968; Yom-Tov, 1971a, 1971b; Schmidt-Nielsen *et al.*, 1971; and others). In aestivating ampullariids, *Pomacea lineata* can tolerate a loss

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of over 50% of its tissue weight (Little, 1968) while *Pila virens* dies when 50% of its tissue water has been lost (Meenakshi, 1964). Also, metabolism during aestivation in snails belonging to the family Ampullariidae has received attention. The Indian ampullariid, *Pila virens,* has been shown to be anaerobic (Meenakshi, 1956, 1957, 1964) and the African ampullariid, *Pila ovata,* has been shown to be aerobic (Visser, 1965; Coles, 1968, 1969) during aestivation. Such differences raise questions about metabolism as well as water economy and temperature regulation in a neotropical ampullariid like *Pomacea urceus.*

Since life history, growth, and biomass production (Burky, in preparation), and buoyancy changes as related to respiratory behavior (Burky and Burky, in preparation) were being studied for *Pomacea urceus,* it was decided to investigate the temperature and water regimes during aestivation and to measure oxygen consumption in active and aestivating snails. The adaptive significance of the data on temperature, water loss, and oxygen consumption is discussed in relation to the annual dry season and to the other existing information on *Pomacea urceus* (Burky, in preparation; Burky and Burky, in preparation).

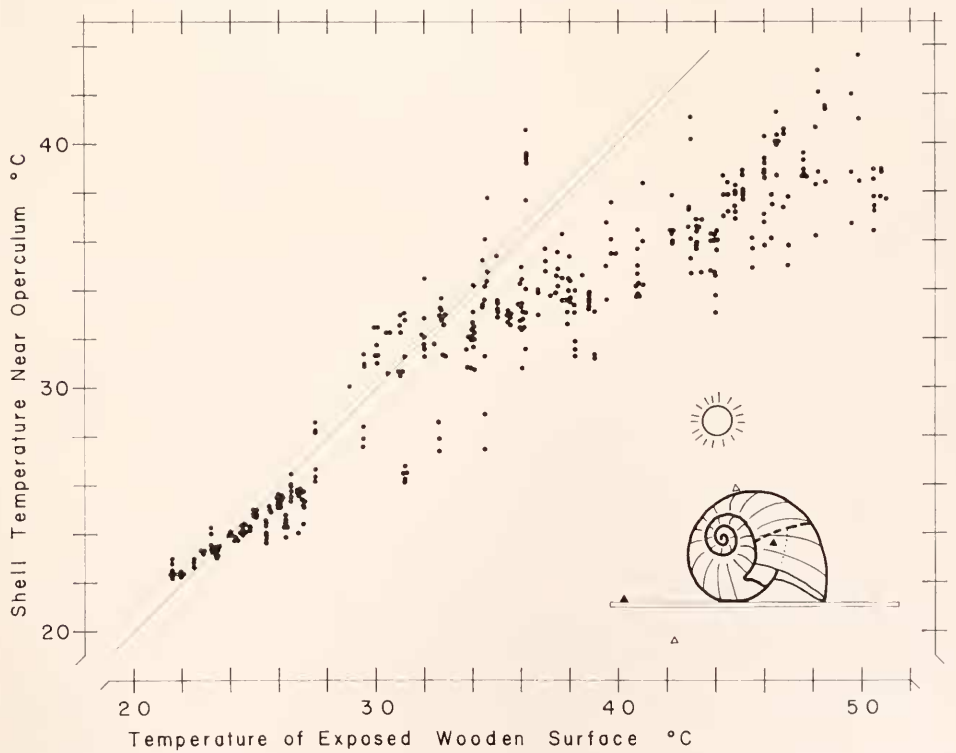


FIGURE 1. Shell temperature near the operculum of *Pomacea urceus* is plotted against the temperature of the exposed wooden surface; snails are experimentally exposed to direct sun during aestivation. The isothermal line is given for reference. The stylized diagram gives the position of an experimental snail in relation to sun and wooden surface. The closed triangles represent the positions of the thermistor probes for the plotted data. The open triangles give the positions of thermistor probes recording the temperatures of shaded air and upper exposed shell surface. For further details, see text.

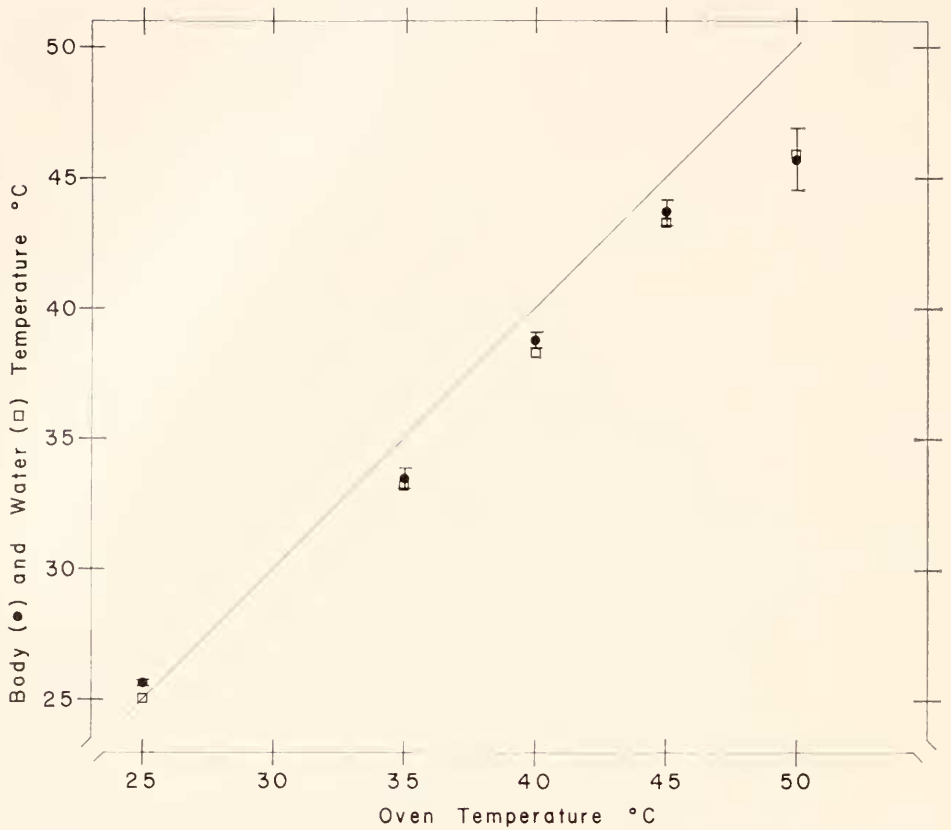


FIGURE 2. Body temperature of *Pomacea urceus* (closed circles) with 95% confidence intervals and the temperature of water in an open beaker (open squares) are plotted against oven temperature. The isothermal line is given for reference. For further details, see text.

## MATERIALS AND METHODS

*Pomacea urceus* was collected in the plains (Los Llanos) region of Venezuela. Field studies were carried out in the local area known as El Estero de Camaguán near the village of Camaguán in Guarico State. Laboratory experiments on temperature and oxygen consumption were carried out on aestivating and active snails collected during the dry and rainy seasons, respectively.

Snails were experimentally exposed to the tropical sun to record their response to the absorption of solar radiation. Aestivating adult snails were placed (aperture opening downward) on a gray wooden surface on a roof terrace of the laboratory in Caracas. Experiments were set up in the morning before the sun was high enough to directly illuminate the experimental area (initially the snails were in the shade). In this way the snails were gradually exposed to the direct tropical sun. During the day the major influences on solar radiation were the passage of clouds and the angle of the rays as the position of the sun changed. Temperatures of shaded air, exposed wooden surface about 25 cm from the snail, upper exposed shell sur-

face, and lower shaded shell surface (columella next to the operculum) were recorded at 20 minute intervals with YSI thermistor probes. The position of these probes is indicated in Figure 1. The shell temperature next to the operculum was chosen as an index of body core temperature because this area was shaded; it was *not* in contact with the wooden surface; it was adjacent to a large volume of tissue; and the probe could be taped to the shell without disturbing the snail or obstructing the movement of the operculum. During aestivation the operculum of a large snail can be withdrawn 3 to 6 cm from the aperture edge of the columella area. At the end of some experiments a small hole was made in the shell (using a ballpeen hammer) and core temperature was recorded (less than 30 seconds needed for this manipulation) with a hypodermic thermistor probe. These core temperatures can then be compared to temperatures taken next to the operculum. The core temperatures of 12 snails average 1.2° C higher than the columella shell temperature (core index) of Figure 1.

Snails were maintained at controlled temperatures so their body temperature could be compared with the temperature of water having a free surface. Groups of five to eight adults were maintained for four hours or longer at oven temperatures of 25, 35, 40, 45, and 50° C. Shell temperature and temperature of water in an open beaker (100 ml—roughly equivalent to snail tissue volume) were recorded at 20 minute intervals until shell temperature was constant for three successive readings. Body core temperature was taken at the end of each experiment; mean values with 95% confidence limits are given in Figure 2.

Field temperatures were taken before the end of the dry season and recorded with YSI thermistor probes. The body core temperatures were taken only after all other values had been recorded. The snails were removed from their positions of aestivation, a hole made, and the thermistor probe inserted (less than one minute needed for this manipulation). The soil moisture content was measured with a soil moisture meter (O.S.K. 450 Riken Moisture Meter, Model R-1-1 Moisture Indicator), a calibrated conductivity determination. These field values are summarized in Table I.

Weight loss during aestivation was measured as an index of tolerance to water loss. For weighing experiments snails were initially maintained in large outside tanks and fed lettuce. Active adults (males and females) were removed from these tanks, drained, weighed, and placed in open cardboard boxes to initiate aestivation. Snails were maintained in the laboratory at room temperature, generally between 20 and 25° C, and weighed at varying intervals. The snails were usually weighed over a period of five days, so a mean date was determined for each weighing. A long term and a short term experiment were started in January 1969 and in February 1970, respectively. Each snail's weight is expressed as a percentage of its weight on the first day of aestivation. The mean percentage and 95% confidence limits have been computed for the snails of each weighing.

The oxygen consumption of aestivating and active snails was measured at 30° C using two plexiglass chambers (1.6 liter) and Warburg manometers (KOH was used for $CO_2$ absorption). One to four aestivating snails could be placed in a chamber while only one active snail could be measured in an experiment. Thirty minutes to an hour was allowed for equilibration and one chamber was used as a thermo-barometer. Readings were taken at about 30 to 60 minute intervals. After

each experiment the shell length, whole animal live weight, body wet weight (no shell), and body dry weight (100° C in an oven until constant weight) were determined (Table II).

## Results

The relationship of columella shell temperature near the operculum (index of core temperature) to exposed wooden surface temperature (25 cm from shell) is shown for 25 individual adult snails (males and females, shell lengths 94 to 129 mm) in Figure 1. The temperatures near the operculum (core index) for exposed wooden surface temperatures above 24–25° C (Fig. 1) were recorded after the snails were no longer in the shade. Those points above the isothermal line were recorded after clouds had obstructed solar radiation and indicates that the wooden surface cools faster than the shell near the operculum (core index). Throughout these experiments the temperature of the upper exposed shell surface (data not given, see diagram of Figure 1) were higher than the temperatures of the exposed wooden surface, due to heat absorption by the dark brown to black coloring of the snail shells. Shaded air temperature (data not given, see diagram of Figure 1) were always 8–10° C lower than those of the shell near the operculum (core index) at higher temperatures (above 35° C). This indicates some heat flow from the snail to the air. During these experiments on aestivating adults, opercular movements (exposure of mantle tissue to air) were commonly observed, particularly at higher temperatures when evaporative cooling can be assumed to be important. All snails survived these experiments. The data of Figure 1 indicates regulation of body temperature, generally below 41° C when animals are experimentally exposed to direct solar radiation.

Figure 2 gives the results of experiments at controlled air temperatures in an oven. The higher body temperatures at 25° C in the oven might be a factor of metabolic heat production. The body core temperatures at oven temperatures of 35, 40, and 45° C were about 0.5° C higher than the water temperatures of open beakers. Snails at 40° C remained in good condition (opercular movements observed) while the bodies of those at 45° C were extended to the edge of the aperture opening with foot tissue visable. The snails at 45° C didn't retract rapidly when touched. The bodies of the snails at 50° C were extended beyond the edge of the shell aperture; they were either moribund or dead after a few hours. This condition is reflected in the large variation in the body temperature of snails at 50° C (Fig. 2) with a mean core temperature which is essentially the same as the temperature of water in an open beaker. These experiments at controlled temperatures indicate an upper lethal temperature between 40 and 45° C and show that evaporative water loss is responsible for lowering body temperature (Fig. 2).

Four groups of 25 aestivating spat (mean shell length about 10 mm and mean weight about 0.3 g) were exposed to the mid-day tropical sun in April 1970. Within 30 minutes all had fluid bubbling from the edges of their opercula. At the end of two hours they were submerged in water and all were dead. Another group (150 spat) was not exposed to the sun and all were active within one hour of submersion in water, some within three minutes. Significantly, adults were exposed to the sun for many days without mortality. Exposure in the field is discussed below.

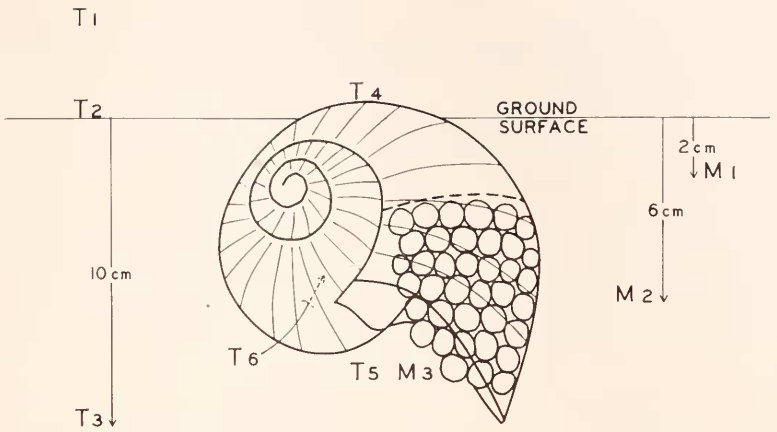


FIGURE 3. The position of a female *Pomacea urceus* (stylized shell) with eggs during aestivation in the field. $T_1$ to $T_6$ (°C) are reference points for temperatures given in Table I and correspond to shaded air, ground surface, soil (10 cm depth) about 25 cm from snail, exposed shell surface, soil beneath snail, and body core temperature respectively. $M_1$, $M_2$, and $M_3$ are reference points for the soil moisture content values of Table I. The depths, shell, and eggs are drawn to scale.

TABLE I

*Temperature and moisture regimes for* Pomacea urceus *during aestivation in the savannah. Temperature (°C—$T_1$ to $T_6$) and soil moisture content (weight ratio—$M_1$ to $M_3$) values correspond to the reference points of Figure 3*

| | Morning (8:15–9:30) May 2, 1970 | | | Mid-day (12:30–14:45) May 1, 1970 | | |
|---|---|---|---|---|---|---|
| | Range | Mean | ±95% confidence limits | Range | Mean | ±95% confidence limits |
| $T_1$ | 31.5–34.0 | 32.71 | ± 1.128 | 35.0–40.0 | 38.17 | ± 1.231 |
| $T_2$ | 32.5–38.5 | 35.57 | ± 2.511 | 42.5–54.5 | 49.61 | ± 3.012 |
| $T_3$ | 27.3–30.2 | 28.66 | ± 1.343 | 29.6–33.7 | 32.02 | ± 0.889 |
| $T_4$ | 32.0–36.5 | 34.09 | ± 1.880 | 42.0–56.5 | 48.69 | ± 3.098 |
| $T_5$ | 27.2–28.6 | 27.97 | ± 0.506 | 31.6–37.5 | 34.01 | ± 1.447 |
| $T_6$ | 27.4–30.7 | 28.91 | ± 1.198 | 34.6–39.3 | 37.51 | ± 1.138 |
| $M_1$ | 40–50 | 44.6 | ± 4.23 | 25–78 | 45.9 | ±15.17 |
| $M_2$ | 50–80 | 70.6 | ±13.02 | 55–82 | 70.3 | ± 6.37 |
| $M_3$ | 69–74 | 72.0 | ± 2.14 | 49–84 | 65.9 | ± 7.55 |

Values for temperatures and soil moisture near *Pomacea urceus* aestivating in the savannah are given in Table I for the reference points of Figure 3. Measurements were taken on seven snails (mean shell length, 116.7 mm ± 9.01 S.D.) during the morning and on nine snails (mean shell length, 105.3 mm ± 10.77 S.D.) during the afternoon. Adult snails normally aestivate with a small patch of shell surface exposed (Fig. 3), and the hard-baked ground has small cracks which ap-

parently form minute air passages to the brood chamber beneath the shell aperture. Figure 3 shows the position of an egg clutch at the beginning of the dry season. At the time of these field measurements (end of dry season), only spat were found beneath females. Soil moisture content increases with depth. However, in the afternoon the soil moisture content immediately below the snails (about 10 cm depth) is somewhat less than at 6 cm. This lower moisture content would suggest evaporative water loss from the soil adjacent to the snails; however, these differences are not significant (Table I). This does not mean that evaporative cooling by the soil is not important. It was not possible to take soil moisture readings at 10 cm depth for comparison with the level immediately below the snails. Also, a certain amount of variation is implicit in these field studies since snails were found

TABLE II

*Oxygen consumption for active and aestivating snails at 30°C*

| | Active | Aestivating |
|---|---|---|
| Shell length (mm) Mean ± S.D. | 110.2 ± 10.64 | 104.7 ± 12.59 |
| Live (body & shell) weight (g) Mean ± S.D. | 294.5 ± 104.18 | 169.6 ± 64.34 |
| Body wet weight (g) Mean ± S.D. | 101.0 ± 36.37 | 58.6 ± 23.58 |
| Body dry weight (g) Mean ± S.D. | 20.7 ± 12.81 | 12.7 ± 4.42 |
| ml $O_2$/hr/mean snail ±95% confidence limits | 5.07 ± 1.458 | 1.05 ± 0.439 |
| µl $O_2$/hr/g wet ±95% confidence limits | 54.57 ± 15.289 | 20.82 ± 12.452 |
| µl $O_2$/hr/g dry ±95% confidence limits | 310.72 ± 73.551 | 91.81 ± 49.902 |

aestivating at varying distances from areas of standing water, and these measurements were taken over periods of one hour 15 minutes and four hours 15 minutes during the morning and afternoon, respectively. At all times the temperature of exposed shell ($T_4$) was higher than body core temperature ($T_6$) due to the absorption of solar heat. The difference between $T_4$ and $T_6$ indicates transfer of heat from the shell surface to the body tissues. In the morning the soil temperature beneath snails ($T_5$) is generally less than the soil temperature at 10 cm depth ($T_3$), thus indicating evaporative water loss (cooling) of the soil adjacent to the snails. In the afternoon the relationship is reversed with $T_5$ greater than $T_3$ indicating transfer of body heat to the surrounding soil at a time of greatest solar absorption. The high shell temperature is a result of the dark brown to black coloration (significance will be discussed). Also, the temperature of exposed shell surface ($T_4$) is greater than the air temperature ($T_1$) indicating heat transfer from the exposed shell surface to the air.

The weight loss during aestivation is given in Figure 4. A long term experiment on 126 snails (mean shell length, 91.5 mm; live weight range, 32.6–288.2 g at start) was terminated 526 days later with 83 living snails. A short term experiment on 41 snails (mean shell length, 100.3 mm; live weight range, 81.5–385.6 g

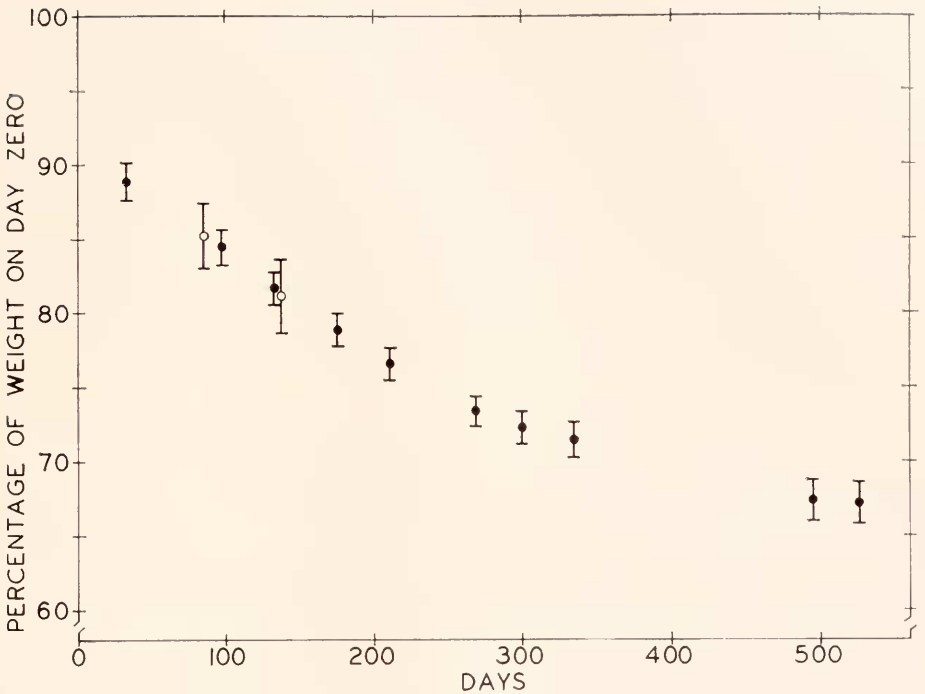


FIGURE 4. Weight loss during aestivation of *Pomacea urceus* in the laboratory is plotted against time. The mean weights of a long term experiment (closed circles) and a short term experiment (open circles) are given with 95% confidence limits. For further details, see text.

at start) was terminated 137 days later with 32 living snails. The loss of snails during the course of these experiments was due to mortality and the utilization of some specimens for other experiments (only one died in the short term experiment). The duration of the short term experiment approximates a normal period of aestivation (about 4.5 months) with 19% weight loss (about 35% of tissue weight). The long term survival (526 days) under these conditions with 34% weight loss (about 62% of tissue weight) is remarkable. This represents an aestivation period of about four times the normal. The initial weight loss is most rapid and represents the laying of eggs by some females and probably the loss of water retained in the mantle cavities of both males and females. On occasion, one of us (A. J. B.) recorded relative humidities as low as 45% and as high as 80% at the laboratory during the dry and rainy seasons, respectively. The weight loss during aestivation would give gross values of between 118 and 233 mg $H_2O$ per day for a snail with a tissue weight of 100 g for the long and short term experiments, respectively.

The oxygen consumption values for 15 aestivating and 18 active *P. urceus* are summarized in Table II. Rates were measured at 30° C since this is within the normal range for body temperatures during aestivation (Table I) and during activity in the rainy season when the diurnal temperature ranges can be 28.6–32.8° C (Burky and Burky, in preparation). The total oxygen consumption for active adults is about five times greater than for aestivating snails. Also, the

values in Table II draw attention to the marked differences in body weights for active and aestivating snails of similar size.

Five aestivating adult snails were placed in each of three sealed desiccators with dial hygrometers: (1) air and $CaCl_2$; (2) KOH, $CaCl_2$, pyrogallol, and replacement of air with $N_2$; (3) same as No. 2 but without KOH. In five days the chamber humidities had risen to 32, 44, and 41%, respectively with activity of two and three snails in chambers (2) and (3), respectively. On day 26 all snails in chambers (2) and (3) were dead. All snails in chamber (1) were living on day 77. Based on the oxygen consumption rates of Table II, chamber (1) contained more than the two liters of air necessary to supply oxygen for these snails. The mortality in the other two chambers indicate that *Pomacea urceus* can not survive for prolonged periods under anaerobic conditions.

## Discussion

As pointed out in the introduction, respiration in ampullariid snails is amphibious. Although many ampullariids are completely aquatic, some are terrestrial for oviposition and/or for aestivation during periodic dry seasons (Prashad, 1925, 1932; Ranjah, 1942; Meenakshi, 1956, 1957, 1964; Coles, 1968; Little, 1968; Burky, in preparation; and others). It follows that temperature regulation for these snails is also amphibious. During the wet season, ampullariids are directly subject to the temperature fluctuations of the water. Prashad (1925, 1932) reports that *Pila globosa* commonly makes long excursions on land and will remain out of water for a few hours to lay eggs, but there is no information on temperature. Apart from this, information indicates that *Pila globosa* (Prashad, 1925, 1932; Ranjah, 1942; Saxena, 1955), *Pila virens* (Meenakshi, 1956, 1957, 1964), *Pila ovata* (Coles, 1968, 1969), *Pomacea lineata* (Little, 1968), *Pomacea depressa* (Little, 1968), and *Pomacea urceus* (Pain, 1950; Burky, in preparation, and this report) are in aestivation for most of their terrestrial phase.

This study shows that *Pomacea urceus* (adults) can regulate body temperature under experimental conditions (Figs. 1 and 2) by exposing foot and mantle through opercular movements. In pulmonate slugs there are additional problems of water loss since there is no shell for protection (Hogben and Kirk, 1944; Dainton, 1954a, 1954b). At controlled temperatures it is indicated that water evaporation from *P. urceus* may be similar to loss from a free water surface. Significantly, evaporative water loss for active *Helix aspersa* is similar to that of a free water surface (Machin, 1964, 1965), but water loss from the mantle of inactive *H. aspersa* can be regulated (Machin, 1965, 1966). Water loss for pulmonate snails under arid conditions is inadequate for temperature regulation (Pomeroy, 1968; Yom-Tov, 1971a; Schmidt-Nielsen *et al.*, 1971). For *Helicella virgata* (Pomeroy, 1968) and for *Trochoidea seetzeni* (Yom-Tov, 1971a) the climbing on vegetation is important for regulation of body temperature. This is a function of their position in the temperature gradient between soil and air. *Sphincterochilla boissieri* survives exposure to the sun on the ground surface of the desert by the high reflectivity of its light colored shell (Yom-Tov, 1971a) and by slow conduction of heat from the substrate (Schmidt-Nielsen *et al.*, 1971). Under field conditions the dark shell of *Pomacea urceus* absorbs solar radiation and heat is transferred to the air and to the body tissues. Heat then flows from the snail to its burrow walls by conduction and subsequently

some heat is dissipated by evaporative water loss from the earth next to the shell (Fig. 3). The water loss during aestivation under experimental conditions (118–233 mg $H_2O$/day/100 g tissue) would be inadequate to be an important factor for sustained temperature regulation in the field. However, the ability to regulate temperature by evaporative cooling could act as a supplement to the cooling afforded by the ground. *Pomacea urceus* can survive 14 months with a loss of 62% of its tissue weight (35% during a normal dry season). *Pomacea lineata* can survive for over 13 months with a loss of greater than 50% of its tissue weight (Little, 1968). Normally, *Pila virens* loses 5% of its tissue water over a six month period, but under experimental conditions (operculum removed) snails die when 50% of their tissue water has been lost (Meenakshi, 1964). Aestivation in *Pila virens* is obviously different since it is found deep in the ground with the operculum and dried mucus sealing the shell opening (Meenakshi, 1964). Meenakshi (1964) also showed that *Pila virens* does not survive at or above 40° C, nor at or below 20° C. The present data on *Pomacea urceus* suggests an upper lethal temperature between 40 and 45° C with temperature regulation generally below 41° C (Table I; Figs. 1 and 3). A lower lethal temperature was not determined but it would not be surprising if it is similar to that found for *Pila virens* since the data of Burky and Burky (in preparation) and Table I indicate that field temperatures for *Pomacea urceus* are normally above 24–25° C.

Excretion must also be considered in water balance. It is known that *Pila ovata* (Visser, 1965), *Pila globosa* (Saxena, 1955; Raghupathiramireddy and Swami, 1963), *Pomacea lineata* (Little, 1968), and *Pomacea urceus* (Pacheco and Pereyra, unpublished data) all excrete uric acid during aestivation. For aestivating *Pomacea urceus* 4.2, 4.4, and 8.1 mg uric acid per gram of fresh tissue are found for hepatopancreas, foot, and kidney, respectively (Pacheco and Pereyra, unpublished data). The water saving advantage of uricotillism during aestivation is apparent.

The exposure of a small patch of the brown to black shell is a seemingly nonadaptive condition. It is known that many snails of deserts have light-colored shells (Morton, 1958; Russell Hunter, 1964; Pomeroy, 1968; Yom-Tov, 1971a; Schmidt-Nielsen *et al.*, 1971) and that this coloring acts to reflect solar energy (Yom-Tov, 1971a). Exposure of the shell by *Pomacea urceus* appears to promote the formation of cracks about the animal as the ground surface dries. These cracks undoubtedly aid in evaporative water loss from the area of the shell and for the diffusion of air (metabolism is discussed below). The dark sculptured shell has a cryptic function since it blends with the ground surface, *i.e.*, visual protection from predation by birds.

Oviposition in *Pomacea urceus* is at the beginning of the dry season after the female has burrowed into the surface mud. Clutches are laid beneath the shell aperture where the spat hatch and aestivate until the rains start about four months later. Camouflage and temperature regulation is apparently important for the protection of spat since they are unable to survive exposure to the tropical sun under experimental conditions (this report) or in the field during the dry season (Burky, in preparation). It is also known that adults reach a shell length of at least 85 mm before going into aestivation at the beginning of the dry season (Burky, in preparation). This suggests that there may be a minimum body volume for maintenance of body temperature and for water balance during the dry season.

Although aestivation in *Pila virens* is anaerobic (Meenakshi, 1956, 1957, 1964), it is aerobic in *Pila ovata* (Visser, 1965; Coles, 1968, 1969) and in *Pomacea urceus*. Further, *Pila virens* accumulates lactic acid during aestivation (Meenakshi, 1956, 1957) while *Pila ovata* (Coles, 1968) and *Pomacea urceus* (0.219 and 0.183 mg lactic acid per gram of fresh tissue for foot and hepatopancreas, respectively; Pacheco and Pereyra, unpublished data) do not accumulate lactic acid during aestivation. The special problems of animals under anaerobic conditions have been discussed (von Brand, 1946; Dales, 1956; Beadle, 1961; and others). Both *Pomacea urceus* and *Pila ovata* (Coles, 1968) have a similar rate of oxygen consumption with the rate during aestivation being one fifth and one sixth that for active snails respectively. In *Pila ovata*, aestivating snails elevate oxygen consumption when disturbed (Coles, 1968). This type of disturbance reaction is undoubtedly true for *Pomacea urceus* since aestivating adults have been observed (by A. J. B.) to extend their body when the shell is knocked. *Pomacea urceus* aestivates next to the ground surface where conditions in the dry soil are probably not anaerobic. The soil cracks around the shell make oxygen more available to the snail. Further, a good oxygen supply is assumed necessary for the developing eggs in the brood chamber beneath the female. In his discussion of anaerobic habitats, von Brand (1946) points out that in most soils the oxygen concentration is sufficient for aerobic respiration. However, after rain when the soil is wet, the exchange of gases with the air is reduced and the ground oxygen can be rapidly depleted. Anaerobic conditions for aestivating *Pomacea urceus* are most likely to occur at the beginning and at the end of the dry season. It would not be surprising if these snails use pulmonary respiration via their siphon when they first burrow into the mud at the water's edge. At the end of the dry season the first heavy rains could fill the burrows and cut off the oxygen supply, but burrows are superficial and anaerobic conditions could involve only a few hours. Also, these snails become active in the presence of water at the end of the dry season. This is particularly rapid in spat since only minutes are necessary for full activity.

Attention has been drawn to the annual sequence of rainy and dry seasons of the Venezuelan plains and to the terrestrial and aquatic phases in the life cycle of these snails. The ampullariid gastropods are doubly adapted in terms of their "amphibious" respiratory structures. The presence of unlimited water or its relative absence provides different conditions for temperature experience and activity. The behavioral adaptation of burrowing and the subsequent inactivity (aestivation with lowered metabolism) are of advantage for survival during the dry season. Further, uricotellism and tolerance of dehydration are both adaptive under arid conditions. The existence of wet and dry seasons stress the importance of adaptations for an amphibious way of life.

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## Summary

1. It has been demonstrated that adult snails generally regulate their body temperature below 41° C under experimental conditions and that their upper lethal temperature is between 40 and 45° C.

2. Field data indicate that under natural conditions adult body heat is transfered to the ground of the aestivation burrow by conduction and that this heat is at least in part dissipated by evaporative loss of soil moisture.

3. Under experimental conditions snails can survive for an aestivation period of four times the normal length and with a loss of 62% of their tissue weight. This level of experimental water loss would be inadequate as the only agent of temperature regulation under field conditions but could be a supplement to heat transfer to both soil and air as well as evaporative cooling afforded by the ground.

4. Aestivating adults can survive many days of direct exposure to the tropical sun (out of burrow) while juveniles are dead within two hours or less.

5. The metabolism of aestivation is aerobic with oxygen consumption about one fifth that of active snails.

6. Females provide protection from high temperatures and from water loss for eggs and spat during the dry season. The adaptiveness of superficial aestivation burrows is discussed in relation to the needs of aerobic metabolism for adults and developing eggs.


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